SUNLIGHT AVOIDANCE COMPARED BETWEEN *HESPEROPSIS GRACIELAE* (MACNEILL) (LEPIDOPTERA: HESPERIIDAE) AND *BREPHIDIUM EXILIS* (BOISDUVAL) (LEPIDOPTERA: LYCAENIDAE)

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Abstract.—Tolerance of solar radiation by the sympatric butterfly species, *Hesperopsis gracielae* (MacNeill) and *Brephidium exilis* (Boisduval), was compared. Adults in varying air temperatures (30–40° C) were exposed to different intensities of direct sunlight (13.8–110 kilolux), and the elapsed response times were recorded when butterflies avoided continued exposure by flying to shade. Avoidance response times (transformed log [$Y + 1$]) were shorter in *H. gracielae* (re-transformed mean = 44 sec) than *B. exilis* (102 sec) across all air temperatures and light intensities. Air temperature (affecting the body-temperature increase needed to stimulate flight) and light intensity (affecting the rate of heating) independently influenced the species' tolerance of sunlight. Avoidance response times decreased linearly with increasing air temperature and hyperbolically with increasing light intensity. Rates of decrease did not differ between species. *Brephidium exilis*'s more prolonged exposure to sunlight contradicts its smaller size and larger ratio of body surface-area : volume (0.99) compared with *H. gracielae* (0.78). *Hesperopsis gracielae* appears physiologically less adapted than *B. exilis* to radiation exposure and more readily exploits shade from its hostplant to maintain a lower body temperature.

Key Words.—Insecta, Lepidoptera, comparative thermoregulation, Hesperiidae, *Hesperopsis gracielae*, Lycaenidae, *Brephidium exilis*.

MacNeill's sootywing, *Hesperopsis gracielae* (MacNeill), is a small (wingspread ≈ 23 mm) dark-brown butterfly (Lepidoptera: Hesperiidae) found along the lower Colorado River and near the river along its tributaries in southeastern California, western Arizona, southern Nevada, and southern Utah (Scott 1986). Two or three generations of *H. gracielae* occur from April to October (Emmel & Emmel 1973, Austin & Austin 1980). Larvae of *H. gracielae* feed only on *Atriplex lentiformis* (Torrey) (Chenopodiaceae), a shrub found in dense clumps along lower Colorado River drainages (Emmel & Emmel 1973). *Hesperopsis gracielae* is more rare than the distribution of its hostplant (Austin & Austin 1980). In Nevada, the butterfly's rarity has afforded the species the conservation ranks of 'G?S1', signifying an unknown global (G) rarity and a state (S) rarity of critically imperiled (< 6 viable occurrences) (K. Goodwin, Nev. Nat. Heritage Program, Carson City, personal communication; also see Master 1991).

Hesperopsis gracielae's distinctive, characteristic tendency of flying within riparian shrubs (MacNeill 1970) suggests the species may limit exposure to direct sunlight (solar radiation) to prevent overheating in the high insolation and summer air temperatures within its range (Wiesenborn 1998). The present study further tests this hypothesis by comparing *H. gracielae*'s avoidance of sunlight with that of the pigmy blue, *Brephidium exilis* (Boisduval). *Brephidium exilis* (here ssp. *exilis*) is a smaller (wingspread ≈ 16 mm) brown and white butterfly (Lepidoptera: Lycaenidae) sympatric with *H. gracielae* (Scott 1986). Although *H. gracielae* and *B. exilis* larvae both feed on *A. lentiformis* and are found along and near the lower

Colorado River, *B. exilis* is less specialized, occurring in other low-altitude, alkaline habitats and feeding on other Chenopodiaceae (Scott 1986).

MATERIALS AND METHODS

The study site was located on the eastern edge of the Muddy River floodplain at an elevation of 450 m near Bowman's Reservoir, Clark County, Nevada. Average daily maximum air temperatures at Logandale near the site during 1968–1992 in April, May, June, July, August, and September were 26.5, 31.8, 37.9, 40.7, 39.1, and 35.5° C, respectively (Nat. Oceanic & Atmospheric Admin., Western Regional Climate Center, Reno, Nevada). The site supported a narrow, linear band of *A. lentiformis* with a lesser amount of *Pluchea sericea* (Nuttall). Both *B. exilis* and *H. gracielae* were frequently observed flying among the *A. lentiformis* shrubs throughout the day.

The species' avoidance of direct sunlight was determined similar to the method used previously (Wiesenborn 1998). Insects were individually captured with an aerial net and placed into a shaded 31 cm × 31 cm × 31 cm aluminum-frame cage. The cage was covered on the bottom and on two sides with 13-mesh/cm plastic screen, on one side with aluminum, on the top with clear vinyl, and on one side with a cloth sleeve for inside access. The insect was allowed to acclimate for 5 min, and the cage was repositioned with its aluminum side shaded and direct sunlight transmitted through the top to illuminate one-half of the cage bottom. A 10-cm long *A. lentiformis* branch with 4–5 leaves was placed under the insect at the beginning of each observation. The insect was allowed to walk or fly onto the branch and placed in shade on the cage bottom for 1 min. Insects that flew from the branch before the 1-min shading period had elapsed were placed back onto the branch and the 1-min period repeated. The branch then was picked-up and the insect exposed to direct sunlight passing through 8-mesh/cm organdy cloth laid atop the cage. By using organdy cloth in layers (1, 2, 4, 8, or 16 layers), light intensity striking the insect was varied without altering the sunlight spectrum transmitted. Differences in basking posture required *B. exilis* to be exposed laterally and *H. gracielae* dorsally, and the former's walking required the branch to be continually moved to maintain a constant lateral exposure. The time was recorded when the exposure was begun and when the insect flew from the branch. Subtracting the former from the latter calculated the elapsed avoidance response time in seconds. Observations were stopped after 20 min if flight did not occur (2 of 70 observations, both of *B. exilis* shaded by the 16-layer treatment). Flights from the branch always were to shade.

Each trial consisted of each light-intensity treatment tested once in random order on an insect. Species were tested in random order with both species tested once on 22 April and twice on 23, 24, and 28 April 1998. Trials were performed under 0–5% cloud cover between 10:14 PDT and 15:35 PDT and lasted 15–68 min each. Relative humidity was 18–38% and wind speed 0–5 kmph. Light intensity (measured with a Sekonic L-398 light meter) inside the cage was 4.1–10 kilolux (klx) in shade and 103–120 klx in sunlight without shading by organdy cloth. Air temperature in shade and light intensity beneath the organdy cloth were measured inside the cage at the beginning of each observation.

Two *H. gracielae* and all seven *B. exilis* were collected after being tested. Thoracic and abdominal widths (at midpoints) and lengths were measured with

an ocular micrometer and used (assuming a cylindrical shape) to calculate thoracic and abdominal surface areas (excluding cylinder ends), volumes, and area : volume ratios. Ratios likely represent the effect of body size on heating rate, because surface area would affect the amount of radiation absorbed, and volume would affect the mass being heated. Collected specimens were verified as to species and deposited as vouchers (G. Austin, Nev. St. Mus., Las Vegas, personal communication).

Avoidance response times were transformed log $(Y + 1)$ and analyzed by multiple regression with cage air temperature, light intensity, and species as independent variables (the latter as an categorical variable, Myers 1986). The regression was improved (r^2 maximized and residuals most-randomly scattered) by transforming light intensity $1/X$. Cage air temperature was not related (F = 1.66; df = 1,68; P = 0.20) to light intensity. The interactions species $\times$ light intensity, species $\times$ air temperature, and air temperature $\times$ light intensity were individually added to the regression model and tested for significance ($P < 0.05$). For presentation, transformed avoidance response times were adjusted (Sokal & Rohlf 1981) for transformed light intensity, then retransformed and plotted on logarithmic scale against air temperature. Similarly, transformed avoidance response times were adjusted for air temperature, then retransformed and plotted on logarithmic scale against light intensity. Regression lines were fitted to transformed data for each species and plotted after retransformation.

RESULTS

Combined thoracic and abdominal surface areas were 22 $\pm$ 2.5 mm^2 (mean $\pm$ SD; n = 7) in *B. exilis* and 48 $\pm$ 4.8 mm^2 (n = 2) in *H. gracielae*, and combined thoracic and abdominal volumes were 22 $\pm$ 4.2 mm^3 in *B. exilis* and 61 $\pm$ 7.2 mm^3 in *H. gracielae*. Area : volume ratios were 0.99 $\pm$ 0.096 in *B. exilis* and 0.78 $\pm$ 0.014 in *H. gracielae*, 1.3 times greater in *B. exilis* than in *H. gracielae*.

Avoidance response time was related to air temperature (F = 34.4; df = 1,66; $P < 0.001$), light intensity (F = 99.2; df = 1,66; $P < 0.001$), and species (F = 30.0; df = 1,66; $P < 0.001$). *Hesperopsis gracielae* sought shade earlier (retransformed mean = 44 sec) than *B. exilis* (retransformed mean = 102 sec), and both species sought shade earlier with increasing air temperature (Fig. 1A) and light intensity (Fig. 1B). After accounting for these variables, interactions were not evident between species and air temperature (F = 0.327; df = 1,65; P = 0.57) or species and light intensity (F = 2.52; df = 1,65; P = 0.12). The regression lines in each plot (Fig. 1) therefore do not statistically diverge from parallel; the two species did not differ in their rate of decrease in avoidance response time as air temperature or light intensity increased. Air temperature and light intensity also did not interact (F = 0.26; df = 1,65; P = 0.61), indicating independent effects on avoidance response time. Regression (F = 46.3; df = 3,66; $P < 0.001$; r^2 = 0.68) of avoidance response time on air temperature, light intensity, and species (*B. exilis* = 1, *H. gracielae* = 2) produced the following equation (coefficients $\pm$ SEs):

$$\log (s + 1) = 4.9 \pm 0.5 - 0.086 \pm 0.015 \ (^\circ C)$$
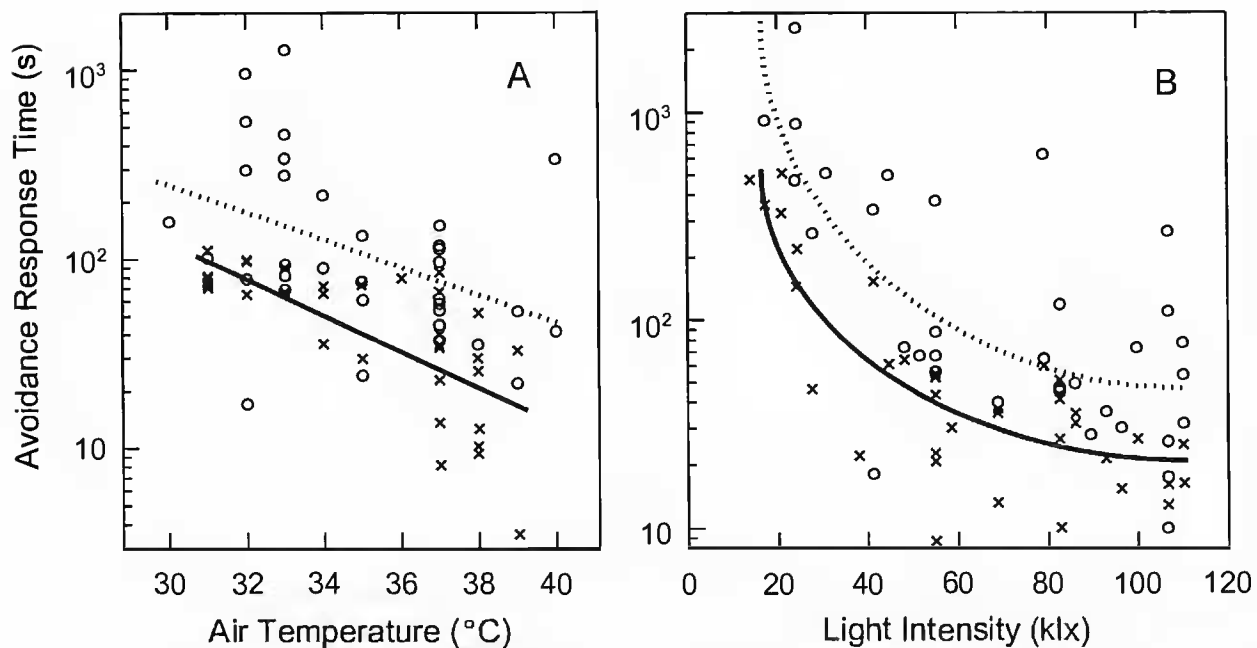$$+ 29 \pm 3 \ (1/klx) - 0.44 \pm 0.08 \ (species)$$

Figure 1. Avoidance of sunlight by *Brephidium exilis* (circles and broken lines) and *Hesperopsis gracielae* (X's and solid lines): avoidance response time in seconds elapsed (A) adjusted for light intensity (transformed $1/X$) and plotted against air temperature and (B) adjusted for air temperature and plotted against light intensity. Avoidance response times, plotted on logarithmic scales, were retransformed to original scale after adjusting transformed log $(Y + 1)$.

DISCUSSION

Flight from sunlight to shade by *H. gracielae* and *B. exilis* likely was a behavioral response to prevent overheating (Wiesenborn 1998); continual exposure to sunlight elevated body temperatures until a threshold was reached stimulating flight to shade. Although body temperatures in butterflies increase as the time of exposure to sunlight increases, the rate of temperature increase diminishes as body temperatures asymptote near an upper limit (Heinrich 1972, 1986; Wasserthal 1975). The curvilinear, asymptotic relationship described in these studies suggests body temperature increases linearly with a proportional increase in exposure time, a function linearized by transforming exposure time log X (Sokal & Rohlf 1981). The log $(Y + 1)$ transformation of avoidance response time (exposure time until flight to shade) in the present study therefore agrees with the diminishing rate of body temperature increase as previously determined.

The hyperbolic relationship between transformed avoidance response time and light intensity (Fig. 1B) likely resulted from the latter being a rate (quantity per time), equal to light energy per area illuminated per time. Rates frequently plot as hyperbolic curves that are straightened by reciprocal transformation (Sokal & Rohlf 1981).

The independent effects of air temperature and light intensity on avoidance response time indicate these variables acted on the butterflies by different mechanisms. Air temperature, approximating the initial body temperature prior to exposure to sunlight, contributed additively towards the body temperature increase required to reach the threshold to stimulate flight. Light intensity, approximating solar radiation, provided the sole energy influx driving body temperature upward. Within species, higher light intensity resulted in greater rate of energy absorbance and greater rate of temperature increase towards the flight threshold. Insect species with greater rates of radiation absorbance heat more quickly as radiation intensity increases (Digby 1955). *Hesperopsis gracielae* and *B. exilis* appear not to differ

in radiation absorbance, because their rates of decrease in avoidance response time did not differ with increasing radiation intensity.

Earlier flight to shade by *H. gracielae* due to greater energy absorbance and body heating rate also is contradictory to the species' larger body size, as larger insects exposed to radiation typically heat more slowly (Heinrich 1986). *Brephidium exilis*'s greater area : volume ratio expectedly would have caused it to heat 1.3 times faster than *H. gracielae*. Instead, *B. exilis* remained, while exposed to sunlight, 2.7 times longer than *H. gracielae*. Because heating rate does not appreciably differ between lateral and dorsal basking (Heinrich 1986), it is unlikely *B. exilis*'s greater tolerance of direct sunlight is due to this behavioral difference. *Hesperopsis gracielae*'s earlier flight to shade may have been due to its darker coloration, increasing radiation absorbance. However, coloration incompletely indicates the proportion of radiation absorbed, because visible light reflected off the insect does not include the near-infrared, part of the spectrum that can contribute significant warming (Heinrich 1972).

Equivalent heating rates between the two species would require *H. gracielae* to have a lower flight threshold, or temperature tolerance, compared with *B. exilis*. The difference between the species' flight-threshold temperatures can be estimated from the plot of avoidance response time against air temperature (Fig. 1A). The mean avoidance response time (retransformed = 67 sec) for both species corresponds to an air temperature of 33° C for *H. gracielae* and 38° C for *B. exilis*. The two species would have responded at the same time if subjected to these two air temperatures and exposed to the same light intensity. The 5° C air temperature difference between species therefore estimates the difference between flight-threshold temperatures; *B. exilis* tolerated body temperatures 5° C higher than *H. gracielae* assuming equivalent heating rates. *Brephidium exilis*'s tolerance of high body temperatures resembles that found in dragonflies, where desert species tolerate body temperatures 4–9° C higher than species found in cooler regions (Polcyn 1994).

Hesperopsis gracielae is less able to tolerate direct sunlight and therefore less adapted to the high insolation and air temperatures of its environment. Rather than tolerating high body temperatures, *H. gracielae* appears to maintain lower body temperatures by flying within the shade of its hostplant, *A. lentiformis*. Thus *H. gracielae*'s specialization on *A. lentiformis* may in part be due to its need for a foodplant providing adequate canopy cover. This concept is supported by considering *Hesperopsis alpheus* (Edwards), a species closely related to *H. gracielae* that is more widely-distributed and feeds on *Atriplex canescens* (Pursh) Nuttall (MacNeill 1970). Of the two insect species, only *H. gracielae* inhabits the lower Colorado River, while *H. alpheus* is limited to higher elevations (> 1500 m) and cooler climates (Emmel & Emmel 1973; G. Pratt, UC Riverside, personal communication). Both *Atriplex* species are found in the lower Colorado River habitats of *H. gracielae* (Turner et al. 1995). *Atriplex lentiformis* is up to 1 m taller than *A. canescens* and provides a more dome-shaped canopy (Turner et al. 1995); *H. gracielae*'s exploitation of *A. lentiformis*'s greater cover likely allows the insect to inhabit an otherwise inhospitable climate. Indeed, *H. alpheus* does not exhibit *H. gracielae*'s habit of flying for prolonged periods within shrubs (MacNeill 1970).

In contrast to *H. gracielae*, *B. exilis*'s wide host range does not allow it to

consistently utilize host shade as a means of thermoregulation, instead requiring the species to be physiologically better adapted to desert climate. For example, one of *B. exilis*'s most-used hosts is *Atriplex semibaccata* Robert Brown (Emmel & Emmel 1973), an exotic plant common at low elevations whose prostrate growth form (Munz 1974) would offer butterflies little protection from sunlight. Tolerance of direct sunlight expectedly also is required by *B. exilis*'s migratory behavior (Scott 1986), reducing the species' ability to remain sheltered within plants.

Conservation activities intended to benefit *H. gracielae* should consider the species' requirement for cover. In addition to furnishing its other life requisites, such as nectar sources for adults (Wiesenborn 1997), restored or preserved riparian habitat should provide *A. lentiformis* patches large enough, and contiguous enough, to allow prolonged flight within host canopies. It is unclear if neighboring, alternative plant species of adequate canopy would by themselves satisfy the insect's shade requirement, because oviposition behavior and plant cover may be interrelated. Regardless of larval suitability, *A. lentiformis* shrubs offering inadequate canopy may not be selected by ovipositing females.

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